Human Impacts in Pine Forests: Past, Present, and Future*

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Annu. Rev. Ecol. Evol. Syst. 2007. 38:275–97

First published online as a Review in Advance on September 5, 2007

The *Annual Review of Ecology, Evolution, and Systematics* is online at http://ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.38.091206.095650

1543-592X/07/1201-0275$20.00

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Key Words

air pollution, biological invasions, conservation, fire, land use

Abstract

Pines (genus *Pinus*) form the dominant tree cover over large parts of the Northern Hemisphere. Human activities have affected the distribution, composition, and structure of pine forests for millennia. Different human-mediated factors have affected different pine species in different ways in different regions. The most important factors affecting pine forests are altered fire regimes, altered grazing/browsing regimes, various harvesting/construction activities, land clearance and abandonment, purposeful planting and other manipulations of natural ecosystems, alteration of biotas through species reshuffling, and pollution. These changes are occurring against a backdrop of natural and anthropogenically driven climate change. We review past and current influence of humans in pine forests, seeking broad generalizations. These insights are combined with perspectives from paleoecology to suggest probable trajectories in the face of escalating human pressure. The immense scale of impacts and the complex synergies between agents of change calls for urgent and multifaceted action.

INTRODUCTION

Pinus is arguably the most important genus of trees in the world. Extensive natural forests and woodlands throughout the Northern Hemisphere are dominated by pines, from subtropical to subarctic latitudes and from coastal plains to mountain ranges and high plateaus.

Humans have interacted with pines since early hominids first encountered these trees in the Mediterranean Basin about a million years ago. Ancient Greeks, Romans, and many other civilizations harvested and managed pines extensively all around the Mediterranean in various ways and for many purposes. The economic importance of Mediterranean pines has continued into the modern era. Although the impacts of human activities on pine forests are most obvious in the Mediterranean region (Barbéro et al. 1998, Le Maitre 1998), pine forests in other parts of Eurasia have also been shaped by humans, most prominently within the past century (e.g., the northern part of northeast China; Xu et al. 2002).

Pines were also important forest constituents in much of North America when humans arrived at least 14,000 years ago, and they have remained important ever since (Williams et al. 2004). These trees were exploited for wood, resins, and seeds by pre-Columbian cultures from Central America to the boreal forests of Canada. Large population centers developed in Mexico, northern Central America, and the southwestern United States during the past 2500 years, with strong local impacts on pine forests. In the five centuries since European conquest and colonization, much of the natural vegetation of the Americas has been radically altered by human activities. Pines, valued for naval timbers, naval stores, and construction materials, were harvested in an east-to-west pattern across North America, concurrent with the spread of Euro-American civilization. Harvesting accelerated in the nineteenth and twentieth centuries with the development of steam-powered sawmills and railroad networks, leaving persistent imprints on the landscape.

This review examines the multitude of human-induced impacts on pine forests, deriving some generalizations from examples at localities throughout the range of pines and involving a broad cross-section of pine species. Examples chosen to show how human-driven impacts have had both positive and negative consequences on the extent and condition of pine forests are compiled in an extensive **Supplemental Appendix** available online. (Follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**.) Sixty-two of the 111 species from 14 of the 16 subsections of *Pinus* recognized by Price et al. (1998), whose nomenclature we follow, are cited in the text and **Supplemental Appendix**.

Important changes to pine forests can usually be attributed to one or several of the following factors, with interactions between factors evident in most cases: changes in fire regimes, changes in grazing/browsing regimes, harvesting and construction activities, agricultural land clearance and subsequent abandonment, purposeful planting and other manipulations of natural ecosystems, alteration of biotas through species reshuffling, and anthropogenic pollution. We discuss the most important aspects of each of these categories, as well as some interactions, and consider the implications of apparent trends and likely trajectories of alterations in pine forests and pine abundances with escalating global change. We focus on human impacts on pine-dominated forests within the natural range of *Pinus*. However, pines are also widely planted outside their natural range, notably in the Southern Hemisphere. Such plantings have a wide range of impacts on ecosystems and subsequent human-mediated factors affect many aspects of these plantations. In many areas, plantings have served as sources for the widespread invasion of natural vegetation by pines (Richardson 2006). Such impacts are not covered here.

CHANGES TO FIRE REGIMES

Fire has played a pivotal role in the evolution and spread of pines since they evolved in the early Cretaceous. Many pines have evolved morphological and life-history adaptations to fire, conferring resilience to natural fire regimes. Human-altered fire regimes have had a major impact on vegetation in most fire-prone systems, resulting in dramatic effects on pines throughout their range (Vale 2002).

Early human populations in Europe used fire in their landscapes as far back as 400,000 years ago. Intentional ignitions have been an important source of fire in the Mediterranean Basin and elsewhere in Europe for millennia and have massively influenced the extent and composition of pine forests. *Pinus halepensis*, for example, which is well adapted to frequent intense fires, probably expanded its range in the last century into areas formerly covered with forests of less fire-tolerant trees (Barbéro et al. 1998). The extensive use of fire by humans has a much shorter history in North and Central America (likely less than 10,000 years), but human-induced changes to fire regimes, together with many other impacts, have altered forest structure and dynamics over wide areas, with particularly dramatic impacts accumulating since Euro-American settlement (Covington & Moore 1994, Mitchell et al. 2006).

In many parts of the natural range of pines, human activities have increased fire frequencies (Agee 1998). In Central America, Mexico, and Southeast Asia, this has often arisen through the agency of swidden agriculture, which has led to the expansion and increased abundance and range of pines in some areas, e.g., for *P. kesiya* and *P. merkusii* in mainland Southeast Asia (Werner 1993), but in most cases such land use has reduced pine cover, as in Central America (Perry 1991). Euro-American settlement of the Rocky Mountains in the mid-1800s, and associated climatic variability, led to a marked increase in fire frequency, which left a legacy of dense, even-aged stands in montane *P. ponderosa* forests (Veblen et al. 2000).

Heavy grazing of rangelands has reduced fire frequency in many parts of the American West by reducing fuel loads, and this has had a major impact on vegetation dynamics (e.g., Belsky & Blumenthal 1997). However, grazing may also allow flammable grasses to invade open pine forests, thereby increasing fire frequency. Fires have been purposefully excluded from pine forests in several parts of the Northern Hemisphere. This situation and its short- and long-term impacts have been best documented for North America (e.g., Gruell et al. 1982, Parsons & DeBenedetti 1979). *Pinus palustris* forests of the southeastern Coastal Plain, sustained by high-frequency

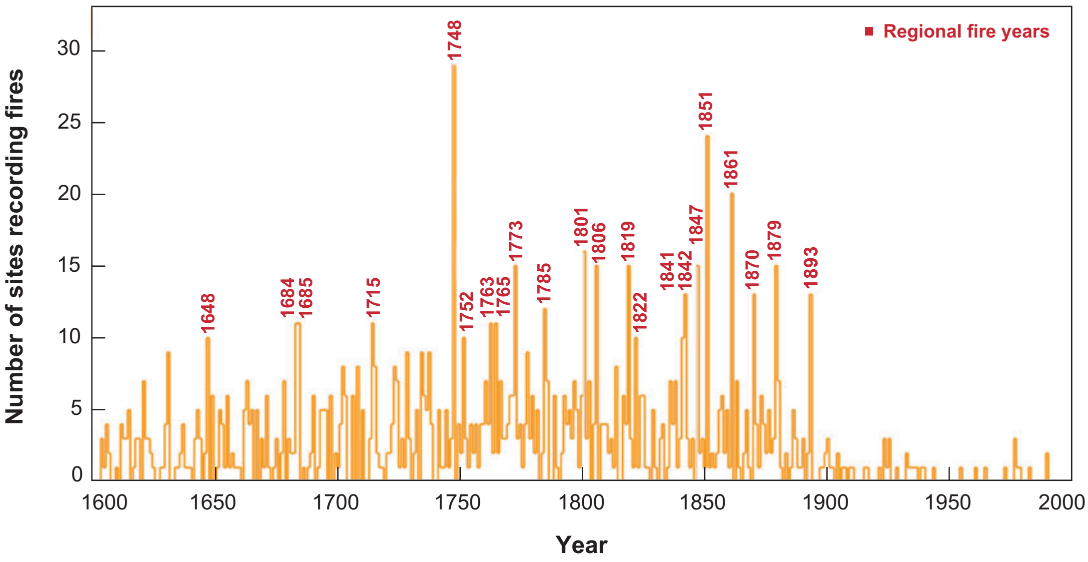

Figure 1

Fire history in southwestern forests and woodlands of the United States from 1600 to the present based on composite fire-scar chronologies from 55 sites in Arizona, New Mexico, and northern Mexico (adapted from figure 5 of Swetnam et al. 1999). Most of the sites were *Pinus ponderosa* forest, or mixed conifer forests with substantial *P. ponderosa*. The y-axis indicates the number of sites with evidence of surface fires in each year. The specific years noted as "Regional fire years" were those in which 10 or more fires occurred among the sites. Fire occurrences before ca. 1900 were controlled primarily by El Niño-Southern Oscillation variation, which governs fine-fuel accumulation (i.e., understory and savanna grasses) and fire-season drought. The dramatic decrease in regional fire frequency in the early 1900s is correlated with intense livestock grazing, which reduced fine fuels, followed by continued grazing and fire-suppression practices.

surface fires, are being replaced by dense slash pine and oak forests in the absence of fire, with consequences for biodiversity, endangered species, and timber production (Kirkman & Mitchell 2006, Mitchell et al. 2006). *Pinus ponderosa* forests in the southwestern United States have been radically altered by Euro-American land uses, including livestock grazing, fire suppression (**Figure 1**), and logging. Dense thickets of young trees now abound, old-growth stands and biodiversity have declined, and human and ecological communities are increasingly vulnerable to destructive crown fires (Allen et al. 2002).

Fire exclusion has allowed pines to spread into some areas where the natural fire regime formerly excluded them (e.g., parks and grasslands of semiarid regions) and has changed forest composition in others (e.g., the southeastern longleaf pine forests). Some impacts of fire suppression in pine forests arose through the disruption of complex relationships between pines, fire, pathogens, and insects (de Groot & Turgeon 1998, Harrington & Wingfield 1998).

GRAZING AND BROWSING

Altered grazing pressure has triggered changes in pine distribution in many regions, but this phenomenon has been best studied in arid and semiarid regions of North America. Changes in stocking rates may initiate, sustain, or halt range expansions, depending on the circumstances. Grazing may interact with climate change, fire, and invasive species, but in all cases the proximal impact is on pine-seedling establishment. Moderate to heavy grazing often facilitates seedling recruitment by reducing grass cover. Local expansion of pine populations has been documented for grasslands, meadows, and steppe. Evidence that pine recruitment decreases when herbivores are excluded lends additional support to the notion that grazing at intermediate levels favors pine expansion (Richardson & Bond 1991). Areas subjected to heavy grazing may remain susceptible to pine colonization long after grazing pressure has been reduced or eliminated.

The expansion of pinyon pines, notably *P. edulis* and *P. monophylla*, in the semiarid southwest of North America during the twentieth century has been attributed to grazing. The debate on whether pinyons have indeed invaded millions of hectares of former grassland or shrubland, or whether this "invasion" constitutes the reestablishment of woodlands on sites from which trees were eliminated or greatly reduced by human activities, has continued for decades. Richardson & Bond (1991) summarized the invasion scenario, Lanner (1981) provided a thorough criticism of the rationale behind such views, and West (1988) gave a good general account of human-induced changes to pinyon-juniper woodlands. However, recent woodland expansions have occurred against a backdrop of long-term climate variation and range expansion (e.g., Gray et al. 2006, Lyford et al. 2003).

Rabbits have influenced pine regeneration in many areas (e.g., *P. sylvestris* in Britain; see **Supplemental Appendix**). Introduced goats have severe impacts on pine regeneration in many areas. In at least one case (*P. radiata* var. *binata* on Guadalupe Island), such impacts are threatening the continued survival of a pine taxon (see **Supplemental Appendix**). There are, however, still relatively few published accounts of changes in pine distribution or density as a result of browsing, perhaps because marked increases in the density of browsers are relatively recent in many areas. Browsers do most damage to young trees rather than mature ones, and the damage to forest composition is not readily visible. The primary effect of changes such as increased moose densities in *P. sylvestris* forests in Sweden are therefore on rates of recruitment to adult growth stages (Edenius et al. 1995). There are thus substantial time lags between changes in browser density and conspicuous change in forest structure. The literature on the impacts of grazing and browsing on pines is therefore biased in favor of cases that lead to range expansions, which are much more obvious.

HARVESTING

Humans have harvested pines and their products for thousands of years. Four categories of harvesting activities have clearly influenced pine forests. These are: harvesting of nuts; fuel wood gathering; logging of pines; and logging of broad-leaved trees.

The harvesting of pine seeds (nuts) for human consumption has a very long history and has been documented for at least 29 pine species (Kunkel 1984), including *P. cembra*, *P. koraiensis*, *P. pinea*, and *P. sibirica* in Eurasia and *P. coulteri*, *P. lambertiana*, *P. sabiniana*, and all of the pinyons in Central and North America. In some societies, pine seeds from natural forests are a crucial economic resource. For example, during good years, the harvest of *P. gerardiana* seeds provides income for about 13,000 people in the Suleiman Mountains of Pakistan (Martin 1995). In the Indian part of its range, such intense harvesting of *P. gerardiana* seeds and browsing by sheep and goats prevent regeneration (see **Supplemental Appendix**). *Pinus maximartinezii* is in danger of extinction in its tiny Mexican range, where nut collectors often lop off whole branches from trees to collect cones (Styles 1992). Fire, together with browsing by goats, donkeys, and cattle, add to the precarious conservation status of this pine (Martin 1995).

Almost all pine species have been used as fuel wood for centuries (examples in **Supplemental Appendix**). Wood harvesting for fuel has impacted pine populations on local to regional scales. Reduction or extirpation of pinyon populations as a result of firewood harvesting by Native Americans has been well documented, most notably in New Mexico (Betancourt & Van Devender 1981). Recent pinyon expansions in some areas may represent a rebound from harvesting, although climate change and grazing are also implicated. The need for fuel wood in many parts of the natural range of pines still accounts for a large part of the total area of pine forest cleared every year. The situation with respect to fuel wood resources in some developing countries is desperate; see for example Perry's (1991, p. 211) chilling account of the situation in El Salvador. Fuel wood use affects pines as much as any group of trees, despite the fact that pine resin makes them less desirable than hardwoods for use in ovens and fireplaces. The ecological consequences of fuel wood gathering, however, can sometimes have differing short- and long-term effects. Fuel wood gathering in plantations of *P. massoniana* in China reduced the growth rate of mature pines but increased regeneration through enhanced seedling establishment (Kong & Mo 2002).

Le Maitre (1998) discussed the history of logging of pine forests of Europe to supply timber for construction and shipbuilding. Historians have been debating the impact of this logging on the extent of the forests over the whole Mediterranean Basin. There is, however, no doubt that these activities had substantial impacts in many areas (Thirgood 1981). The examples in the **Supplemental Appendix** illustrate a wide range of influences of pine logging in other parts of the world. There is an extensive literature on the history, policies, politics, and practices of logging in different parts of the range of pines. A good example of the complexity of the relationship between logging impacts and vegetation structure is described by McDonald (1976) for a Californian mixed conifer forest. Logging and harvesting of pines for timber and naval stores in southwestern Florida during early European colonization resulted in a dramatic decline in populations of *P. palustris* and, to a lesser extent, *P. elliottii* (Walker 2000).

Special attention has been given in recent decades to assessing the impacts of various logging strategies on animals associated with pine forests. Two bird species especially well studied in North America are the red-cockaded woodpecker (*Picoides* *borealis*) and Kirtland's warbler (*Dendroica kirtlandii*). The former species is associated with mature forests of *P. echinata*, *P. elliottii*, *P. palustris*, and *P. taeda* in the southern United States, and the latter inhabits young *P. banksiana* forests in Canada and parts of the northern United States. Harvesting of these pine forests and changed fire regimes have altered the pine age structure, jeopardizing bird populations. The many published studies of the habitat requirements of these species, and of the measures required to ensure their survival (Probst & Weinrich 1993; Wilson et al. 1995), provide valuable models for the study and management of other threatened animals associated with pine forests.

In many areas, logging of trees other than pines has had a major influence on pine forests. For example, the clearing of broad-leaved forests in parts of Asia has created suitable conditions for pines, allowing species such as *P. massoniana* and *P. yunnanensis* to expand their ranges.

RURAL EXODUS AND ABANDONMENT OF AGRICULTURAL LAND

Pines have spread into lands following the abandonment of thousand-year-old agriculture in many parts of their natural ranges in the Old World. Pine forests in central Japan, for example, increased with abandonment of agriculture in hilly areas between 1880 and 1980 (Fujihara & Shirai 2001). Many studies have also documented the spread of pines and other trees onto abandoned farmlands in the southeastern United States. Pines, notably *P. taeda*, usually invade such sites within 10 years of abandonment and rapidly form closed stands that are gradually replaced by hardwoods in the absence of major disturbance (e.g., Golley et al. 1994). Similar trends are evident from nearly all parts of the range of pines.

PURPOSEFUL MANIPULATION

Pines have been widely used and planted in the Mediterranean Basin since prehistoric times. Le Maitre (1998) reviewed how this practice has influenced the distribution of *P. brutia*, *P. halepensis*, *P. pinaster*, and *P. pinea*. Other examples (see **Supplemental Appendix**) range from the local planting of pines by Native Americans, which probably had little effect on their general distribution patterns, to the establishment of modern large-scale pine plantations, which has led to a huge artificial increase in the area under pines. Widespread planting of pines has also reshuffled genetic material. Large-scale afforestation started in the second half of the nineteenth century in southern Europe (e.g., Vallauri et al. 2002). Sustained, large-scale forestry, however, was not widespread in Europe until the early twentieth century and expanded to other parts of the world only in the second half of the past century (Le Maitre 1998).

ALTERED BIOTA

The human-orchestrated reshuffling of biotas has affected pine-dominated systems through the increased impacts of pathogens, both native and introduced, and invasive alien species. One of the earliest examples of an introduced pine pathogen is that of the white-pine blister rust (*Cronartium ribicola*), introduced to North America through trade in pine seedlings. Despite a vigorous and longlasting effort to eradicate currants and gooseberries (*Ribes* spp.), alternate hosts of the pathogen, this disease continues to have major impacts on several pines in North America (Kinloch 2003). The disease is expected to become pandemic throughout most of the range of *P. lambertiana* and other species within the next 50–75 years, and in conjunction with heavy logging,the rust is already significantly reducing breeding populations (**Supplemental Appendix**). In Glacier National Park, Kendall & Arno (1990) estimated that 90% of *P. albicaulis* trees have succumbed to the rust. Lanner (1996) gives a good account of the actual and potential ecosystem-level effects of the elimination of this species. The disease has now spread to *P. flexilis*, with dramatic mortality throughout Alberta, Montana, and Wyoming at the time this review was written. A second locus of introduction of *Cronartium*, in New England, resulted in the spread of white pine blister rust through much of the range of *P. strobus*. Although the disease has not been as severe (except locally) as on *P. monticola*, the threat of its presence has limited the dissemination of planting stock of this species (R.D. Westfall, personal communication).

The pine pitch canker fungus, *Fusarium circinatum*, was first recorded on various pine species in the southeastern United States in 1946. The disease was not particularly problematic in native pine stands; most damage has occurred in managed forests and seed orchards. In contrast, when the fungus appeared on *P. radiata* in California in 1986, it spread rapidly from roadside and amenity plantings to native populations on the Monterey Peninsula. It is now common and a serious pathogen throughout coastal regions of California from San Diego to San Francisco. The long-term survival of the species in the wild is a matter of much concern.

One of the most devastating diseases of natural pine forests is pine wilt caused by the pine wood nematode (*Bursaphelenchus xylophilus*), vectored by longhorn beetles (Coleoptera: Cerambycidae). This nematode is responsible for devastating losses to native pines in Southeast Asia (Mamiya 1983). The disease was discovered in the United States in 1979 (Dropkin et al. 1982). It is now thought that the nematode was introduced to Japan from North America on pine logs and it was able to develop an association with the native Japanese beetle *Monochamus alternatus*, which apparently invaded the islands as a hitchhiker on imported nematode-infested timber (Dwinell 1997).

Various human activities have exacerbated the problem of native diseases and parasites in pine forests. These include the replacement of disease-resistant species with more susceptible species and fire suppression, which favors alternate hosts (e.g., oaks; *Quercus* spp.) over disease-resistant and fire-tolerant species (e.g., *Pinus palustris*). This problem is exemplified by fusiform rust (*Cronartium fusiforme*) in the southern United States, where the relatively disease-susceptible *P. elliottii* and *P. taeda* were planted to replace the more resistant *P. palustris* following heavy logging of the longleaf pine in the nineteenth century (Harrington & Wingfield 1998). Insect outbreaks are generally more common in human-altered monocultures, although other factors are also implicated (e.g., poor sites conditions and stress caused by drought and/or pollution). In southern Europe, infestations of pines by mistletoe (*Viscum album* subsp.

austriacum) and scale insects (*Matsucoccus feytaudi*) are clearly on the increase as a result of single-species afforestation projects (Vallauri et al. 2002).

The impact of invasive alien plants on native pines is probably much greater than is currently reflected in the literature. In particular, the negative effects of invasive alien grasses on pine regeneration in many parts of the Northern Hemisphere are understated. *Imperata cylindrica*, native to Southeast Asia, is having a profound influence on the dynamics of the pine forests of the southeastern United States (Jose et al. 2002). Such changes certainly alter the fire regime and must significantly affect pine regeneration. Similar impacts probably apply to many other taxa in other regions, and the magnitude of such problems is increasing rapidly as invasive alien plants become more widespread and abundant.

An additional and contrasting concern is that several pine species need to be controlled themselves, or even locally extirpated, given the rapidly changing ecological conditions worldwide and the fact that some of them have become invasive encroachers and even noxious weeds. Where the species are indisputably alien (i.e., introduced far outside their natural range in recent times), the issues are generally clear (Richardson 2006), but when the species are within their natural range, or close to it, issues are more complex.

AIR POLLUTION

Toxic effects of industrial air pollution on forests have been recorded since the nineteenth century in Central Europe (Godzik & Sienkiewicz 1990) as well as the western United States and British Columbia (Miller 1989). Intensive industrialization caused uncontrolled emissions of noxious gases such as sulfur oxides (SO_x), nitrogen oxides (NO_x), hydrogen chloride (HCl), hydrogen fluoride (HF), and industrial dust toxic to vegetation in the vicinity of smelters, mines, and power plants (Krupa 1997). With increasing industrialization, air pollutants were dispersed over larger areas, causing serious regional air pollution problems including toxic effects on pines in Europe and North America (**Figure 2**).

Recently, however, the most widespread air pollution effects on forests have been caused by ambient ozone (O_3), a highly phytotoxic component of photochemical smog. Fowler et al. (1999) project that about 50% of the Northern Hemisphere forests will be affected by toxic levels of O_3 by the year 2100. Long-range transport can result in dispersion of the pollutant over large areas, resulting in phytotoxic concentrations in remote locations such as Siberia or mountainous areas of the western United States.

Pinus halepensis, widely distributed in the Mediterranean Basin, appears to be sensitive to O_3, since symptoms of this pollutant have been observed in Israel (Naveh et al. 1980), Greece (Gimeno et al. 1992), Spain (Gimeno et al. 1992), and Italy (Ferretti et al. 2003). The health of *P. cembra*, an important conifer in the timberline ecotone of the European mountains, has declined over the past decade in the Maritime Alps of southern France (Bianco & Dalstein 1999, Vollenweider et al. 2003) and in the Carpathian Mountains (Manning & Godzik 2004). In both areas, the observed injury in *P. cembra* can be ascribed to the O_3-induced foliar symptoms on older leaves. In contrast, there is no evidence of O_3 injury in the conifers of the timberline ecotone of

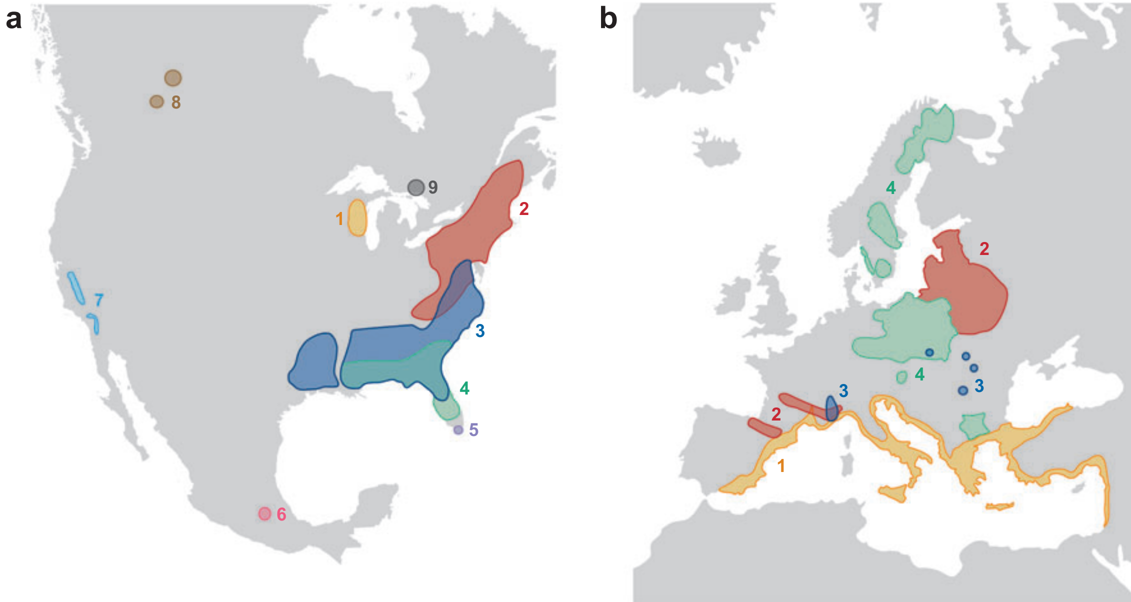

Figure 2

(*a*) Areas in North America where pines are affected by air pollution: (1) Eastern Wisconsin where effects of ozone on *Pinus strobus* have been confirmed, (2) Areas on the East Coast, mostly New England, with suspected effects of ozone on *P. strobus*, (3) Areas in the South where effects on *P. taeda* have been suspected, (4) Parts of the South, mostly in Florida and Alabama, where effects of ozone on *P. elliottii* have been suspected, (5) Area in south Florida with confirmed effects of ozone on *P. elliottii* var. *densa*, (6) Areas near Mexico City with pronounced effects of ozone on *P. hartweggi*, *P. leiophylla*, and *P. montezumae*, (7) San Bernardino and San Gabriel Mountains in Southern California and western slopes of the Sierra Nevada where effects of ozone on *P. jeffreyi* and *P. ponderosa* have been confirmed, (8) Areas in Alberta with effects of sulfurous air pollutants on *P. contorta*, and *P. banksiana* and their hybrids *P. contorta* × *P. banksiana*. (9) Area near metal smelter at Sudbury, Ontario, where SO_2 emissions have affected *P. strobus* and *P. banksiana*. (*b*) Areas in Europe where pines are affected by air pollution: (1) Mediterranean coast areas where ozone affects *Pinus halepensis*, (2) Baltic countries and parts of France and Spain with *P. sylvestris* mildly affected by air pollution, (3) Areas in south-western Alps and the Carpathians with *P. cembra* expressing ozone injury symptoms, (4) Areas in Central Europe and Scandinavia with *P. sylvestris* expressing pronounced air pollution effects.

the central European Alps (Wieser & Havranek 2001), although O_3 regimes are comparable to those in the Maritime Alps (Bianco & Dalstein 1999) and the Carpathians (Bytnerowicz et al. 2002). Other European pine species appear tolerant to ambient levels of ozone.

Pinus ponderosa and *P. jeffreyi* have been affected by O_3 in the western United States, and *P. attenuata*, *P. coulteri*, *P. monticola*, *P. radiata* are potentially sensitive (Miller et al. 1983). Typical effects of O_3 on these species are foliar chlorotic mottle, premature needle senescence leading to crown thinning, and weakening of trees. Severely weakened trees are susceptible to drought and bark beetle attacks, often resulting in the death of the most sensitive individuals (Miller 1989). In the late 1960s, *P. ponderosa* and *P. jeffreyi* were found to be moderately to severely damaged in areas most exposed to O_3 in the San Bernardino and Sierra Nevada Mountains in California (Miller et al. 1983). At present, as the result of several years of drought, long-term effects of air pollution and bark beetle infestations in forests in the San Bernardino Mountains have left millions of dead *P. jeffreyi* and *P. ponderosa* individuals (Keeley et al. 2004). *Pinus strobus* started showing severe symptoms of ozone toxicity over much of the eastern United States in the 1960s (Berry & Ripperton 1963, Rezabek et al. 1989). Sensitive genotypes of *P. strobus* showed reduced photosynthesis, needle necrosis, and decreased height, diameter, and needle length compared to the more tolerant individuals (Irving 1991, Reich et al. 1987). In the South toxic effects of ozone on *P. taeda* have been suspected (Sheffield et al. 1985), and such effects were confirmed for *P. elliotti* var. *densa* (Evans & Fitzgerald, 1993). Forests to the south and southwest of Mexico City have suffered from the effects of urban smog, with some of the highest ambient levels of O_3 in the world. Many *P. hartwegii* and *P. leiophylla* trees showed symptoms of damage similar to those observed on *P. jeffreyi* and *P. ponderosa* in the mountains of Southern California (Miller et al. 2002).

Pines located near metal smelters or power plants can suffer from industrial emissions (**Figure 2**). Known sensitive species in Canada and the northeastern United States include *P. contorta*, *P. banksiana*, and *P. strobus* (Guderian 1977, Legge et al. 1999). *Pinus contorta* and *P. banksiana* hybrids in western Canada have also been affected by SO_2 emissions from extraction of oil from oil sands and gas processing (Mayo et al. 1992). *Pinus sylvestris*, the most widely distributed pine in Eurasia, is well known for its sensitivity to SO_2 (Godzik & Sienkiewicz 1990), HCl, HF (Guderian 1977), and NO_x (Jakubczak & Pieta 1968). The observed crown thinning in this species over large parts of Europe could be partially caused by a synergy between SO_2 and O_3 (Tingey & Reinert 1975). In general, however, the condition of *P. sylvestris* has significantly improved in recent years (Lorenz et al. 2005).

Phototoxic effects of air pollutants have lessened in many European and North American forests because of effective control measures initiated in the 1980s and 1990s against SO_2 and NO_x industrial pollution and the precursors of tropospheric ozone formation (NO_x and volatile organic compounds). With the rapid development of industrial activity in Asia, especially in China, the impacts of industrial air pollution on pine forests will increase (Bytnerowicz et al. 2007).

EFFECTS OF CLIMATE CHANGE ON PINE FORESTS

Pines have been subjected to climatic changes throughout their evolutionary history. The well-documented history of the past 20,000 years, spanning the last glacial-interglacial transition, is especially relevant for understanding the future of pines in the context of ongoing and future global climate change. Some species (*P. banksiana*, *P. sibirica*) have undergone complete geographic displacements since the last glacial maximum 20,000 years ago, whereas others (*P. strobus*, *P. edulis*, *P. ponderosa* var. *scopulorum*) have expanded northward from small, isolated populations to cover vast territories (Jackson et al. 1997, Kremenetski et al. 1998, Lanner & Van Devender 1998). Other species (*P. flexilis*, *P. remota*) have undergone dramatic range contraction and fragmentation in the same period (Betancourt et al. 1990, Lanner & Van Devender 1998). A crucial implication of these patterns is that broad geographic ranges and high abundances provide no guarantee of stability in range or abundance under altered climate regimes of the future.

Seed dispersal was not a major limiting factor to postglacial pine migration; both wind-dispersed (e.g., *P. banksiana*, *P. ponderosa*) and bird-dispersed species (*P. edulis*) expanded their ranges northward rapidly. However, the unprecedented rates of climate change predicted in many future scenarios may outstrip the natural capacity of pines to disperse into newly suitable territory.

Within already established ranges, pine forests have undergone progressive changes in composition and disturbance regime as climate changed. Fire regimes in montane and boreal pine forests have varied dramatically in the past 10,000 years as temperature and moisture regimes changed (Brunelle et al. 2005, Carcaillet et al. 2001). Climate-driven expansions and contractions of pines at upper and lower treeline and at parkland/forest boundaries are well documented (e.g., Lloyd & Graumlich 1997, Lyford et al. 2003, Lynch 1998). Pine populations in forests have increased and decreased in the past few thousand years in response to climate change (Booth & Jackson 2003, Schauffler & Jacobson 2002). Dendroecological studies indicate demographic and fire-regime responses to climate changes over the past few centuries in boreal and montane pine forests and semiarid pine woodlands of North America (Bergeron et al. 2004, Gray et al. 2006, Swetnam et al. 1999).

Ongoing and future climate changes will affect pine-dominated ecosystems in complex ways. Climatic changes will change disturbance regimes, demographic structure, growth rates, and stand composition. Such changes may be under way. For instance, increased radial growth of *P. ponderosa* in the Pacific Northwest of North America observed after 1950, particularly in drought years, has been attributed to increased atmospheric CO_2 concentrations (Soulé & Knapp 2006), and the frequency of large-scale fires has increased in western North American pine forests during the past three decades, corresponding to increasingly early snowmelt (Westerling et al. 2006). Widespread pine mortality events are being induced by the continuing drought in much of the western United States. *Pinus edulis* populations have been decimated over much of the American Southwest as a result of rampant bark beetle infestations in the drought-stressed populations (Breshears et al. 2005). Outbreaks of mountain pine beetle are devastating *P. contorta* populations across wide swaths in western Canada and the United States; these outbreaks are related in part to recent anomalies in winter temperatures (Waring & Pitman 1985). The extensive areas of dead trees increase the risk of wildfire and colonization by invasive species and also alter regional stand age structure.

A longer-term concern is how pines will adjust biogeographically under altered climate regimes. Models of realized distributions of pines species to climate-change scenarios indicate that the ranges of many pine species will be displaced, often dramatically, in a greenhouse world (**Figure 3**). Although these scenarios are probably poorly suited for predicting the future distributions of pines and other species, they provide good indications of the magnitude of biogeographic change that we should

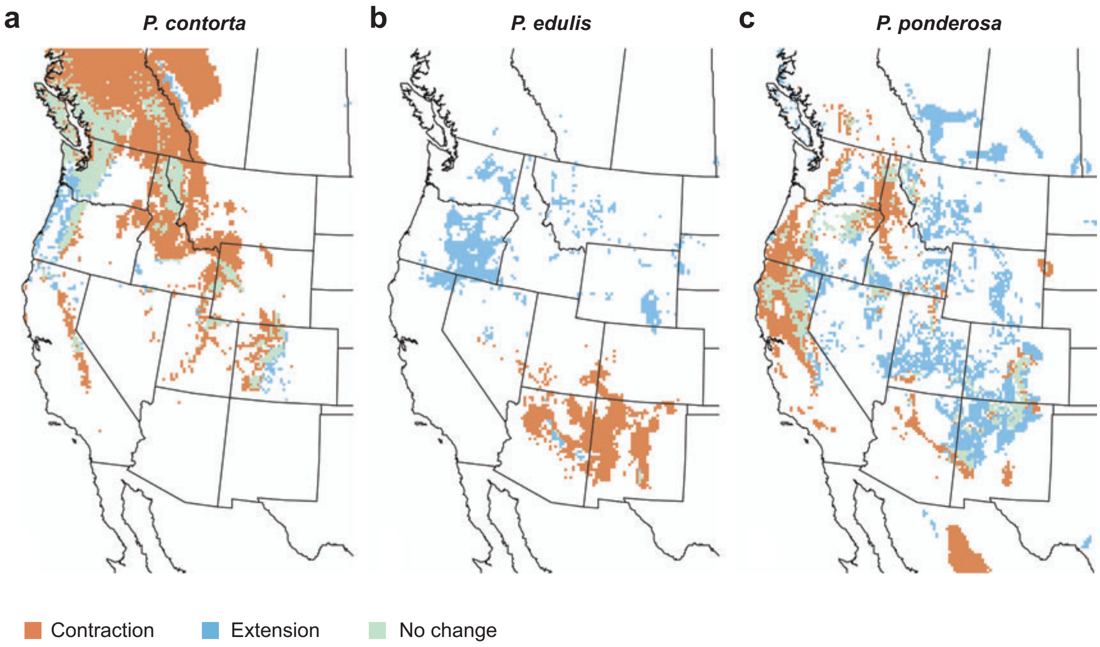

Figure 3

Potential changes in abundance and distribution of three *Pinus* species in response to climate change (Thompson et al. 1998). A regional climate model for the western United States, RegCM (Dickinson et al. 1989), was used to simulate the present-day climate and a simulated climate for the region based on a doubling of the current atmospheric CO_2 concentration. The modern climate and species distributions were used to develop empirical models of the climatic responses of the respective species. These models were used in turn to simulate future distributions under the doubled-CO_2 climate scenario. The distribution of *P. contorta* (*a*) is predicted to shift to higher elevations with a reduction in total area to 35% of its present extent. In contrast, *P. edulis* (*b*) would cover approximately the same land area, but would shift dramatically northward, abandoning nearly all of the territory it currently occupies. *Pinus ponderosa* (*c*) is predicted to move to higher elevations and into the Great Basin, with an overall area expansion of 36%. It is important to note that these shifts in distribution are speculative, because of uncertainties in the accuracy of future climate simulations and the adequacy of the models in simulating the environmental factors controlling species distributions. Also, simulations of this type ignore the potential effects of genotypic variation in determining how species will respond to climate change (e.g., Norris et al. 2006). However, the simulations serve to illustrate that *Pinus* forests will likely experience dramatic changes due to climate change and that the magnitude and direction of the effects will differ between species.

expect. The models ignore the underlying genetic diversity that may play an important role in the ability of pines and other species to adjust to climate change (Rehfeldt et al. 2001). Greenhouse gas climate change may cause novel climates to appear across broad regions (Williams et al. 2007). These changes will probably cause the disappearance of some extant communities and the emergence of novel communities, as has occurred before (Jackson & Williams 2004). Predicted climates for the near future are in some cases as different from today's climate as those of the last deglaciation (Jackson & Williams 2004, Williams et al. 2007)—a time when many pines that are abundant now were rare, and other pines that are scarce now were abundant.

CONSERVATION AND RESTORATION EFFORTS IN PINE FORESTS

The growing pressure from logging and land-use changes is rapidly eroding the genetic diversity of pines. At least one-third of *Pinus* species are either threatened in their entirety or have threatened subspecies or varieties (Richardson & Rundel 1998). Some of these taxa were rare before human intervention (e.g., *P. radiata* and *P. torreyana*), but human activities are threatening other widespread taxa as well, such as numerous tropical and subtropical pines in Central America and Mexico (Dvorak 1990). Although many other pine taxa still occupy large ranges, the loss of specific habitats may threaten their genetic diversity, potentially reducing their ability to respond to changing environmental conditions. Low-elevation populations of *P. ponderosa* in California were eliminated a century ago because they were the most accessible timber sources. Ledig (1993) suggests that the alleles that enabled *P. ponderosa* to survive on dry, low-elevation sites may have been lost when those stands were logged. Low- and middle-elevation populations of many other pine species have been reduced or eliminated as forests have been cut for lumber and firewood and land converted to pasture and crops. In Yunnan Province of China, all but the most inaccessible stands of *P. yunnanensis* and other pines have been cleared to make way for agriculture. In the mid-1960s, 60% of the province was forested, but this figure had dropped to less than 30% by 1985 (H. Hutchins, unpublished information). Similarly, Perry (1991, p. 207) describes the plight of Mexico's forests as follows: "They . . . continue to disappear, first becoming fragmented then reduced to small patches and parcels and finally to small groups of trees on inaccessible mountain slopes and valleys." The net effect of these "secret extinctions" (Ledig 1993) on the ability of species to deal with rapidly changing environmental conditions will never be known, but must be severe. Recent genecological studies of *P. contorta* highlight the importance of genetic diversity in facilitating responses to future climate change (Rehfeldt et al. 1999, 2001).

Pinus pinaster, which occurs in fragmented populations in the western Mediterranean, has had its distribution reshaped and its genetic structure highly modified in the past two centuries by afforestation, especially in France, Spain, and Portugal, as foresters used lineages of different geographical origin (Gonzaléz-Martinéz et al. 2004). A similar situation occurs at the eastern end of the Mediterranean for *Pinus halepensis* (Barbéro et al. 1998).

Hybridization was probably a major factor in the natural diversification of *Pinus* (see e.g., Wang et al. 2001). As in the eastern Mediterranean case cited above, it is likely and perhaps inevitable that pine plantations bringing together lineages from different regions will sooner or later lead to new hybrids. In the native range of the genus, these could potentially alter the genetic structure of natural pine forests on a large scale.

The loss of genetic diversity in pine forests bears directly on human well-being on a global scale. Although tree breeding has already improved productivity (e.g., Lavery & Mead 1998) and disease resistance (Harrington & Wingfield 1998) of pines in exotic plantations, breeders have barely scratched the surface in their efforts to modify pines for human goods and services (Ledig 1998). Clearly, native gene pools, especially of species with commercial importance, need to be conserved if options are to be kept open for further tree breeding selections. Among the economically important (or potentially so) pines of Mexico and Central America, provenances of at least seven species or varieties are threatened. For some species, ex situ gene conservation banks are the only place where these unique gene pools still exist (Dvorak & Donahue 1992). Among the threatened Mexican and Central American pines, *P. tecunumanii*, *P. chiapensis*, *P. greggii*, and *P. maximinoi* have been identified as potential replacements for commercial plantings of temperate pines *P. taeda* and *P. elliottii* in tropical and subtropical regions (Lambeth & McCullough 1997).

Judging from the experience in agriculture, species with less obvious commercial value may nevertheless also be valuable in breeding. An example is *P. washoensis*, a narrow endemic from the mountains on the western rim of the Great Basin in California and northwest Nevada, which persists in a few populations and is on the verge of extinction, largely because of logging in the nineteenth century. Genetic studies suggest that this pine may be a valuable genetic resource for the yellow pines of North America (Niebling & Conkle 1990).

THE FUTURE

We have described some of the many human influences on pine forests. The selected examples show that a wide range of human activities over many centuries have substantially altered pine ecosystems. Many pine species are tenacious, persisting, and even flourishing under severe disturbance regimes. Increasing direct impacts, such as logging and planting, and indirect impacts, such as alteration of disturbance regimes and the composition of biotas, globally increasing ambient ozone and regionally elevated levels of industrial gases and particulate matter, rapidly changing climatic conditions and the further introduction of invasive alien species, including pests and pathogens, are all expected in the future. Such pressures may push many pine taxa beyond their tolerance thresholds.

The immense scale of the impacts and the complex synergies between agents of change call for urgent action on many fronts. For example, (*a*) ecological restoration is increasingly required for almost all pine woodlands and forests to safeguard key ecosystem services. (*b*) Deleterious effects on pine ecosystems of the deliberate or inadvertent reduction of fire frequency must be recognized and effective management strategies devised. (*c*) Relictual fragments of natural pine forests require enhanced protection and reinforcement as well as expansion and reintegration at landscape scales. (*d*) Identification of reference ecosystems as benchmarks will help define appropriate restoration and management goals and facilitate project monitoring and evaluation (Aronson et al. 1995, Egan & Howell 2000, White & Walker 1997). (*e*) Conservation and protection of gene pools is urgently needed for threatened, endangered, and sensitive pine taxa. (*f*) Autecological and synecological information is needed for many narrowly endemic or regionally rare taxa to facilitate conservation and reintroduction efforts. (*g*) Invasive alien pests and pathogens have had huge impacts on native pine ecosystems, and systems to reduce the incidence of new incursions in the future will be essential. (*h*) Interactions among climate change, land use, fire regime, pollution, diseases and pathogens, and invasive species need to be squarely addressed in research and management applications—ecological surprises are inevitable. Instruments for achieving some of these actions are set out in the Conservation Action Plan of the World Conservation Union's Conifer Specialist Group (Farjon & Page 1999).

Efforts are being made to respond to some of these critical needs. For example, Scots pine (*P. sylvestris* var. *scotica*) now occupies only about 1% of its original range in Scotland (Buckley et al. 2001). Forestry Enterprise Scotland has adopted an ambitious approach to active forest management and restoration of both native pine forest and broad-leaved woodland (Peterken & Stevenson 2004). Projects are under way to conserve genetic resources of some of the most threatened tropical *Pinus* species (Dvorak 1990). Examples of the types of field studies needed to provide key autecological and synecological information on rare species are those concerning the Sierra Nevada pine (*Pinus sylvestris* subsp. *nevadensis*) in the mountains of southern Spain (Hódar et al. 2003) and the endemic *P. culminicola* in northeastern Mexico (Jiménez et al. 2005). Kirkman (2005) described landscape-scale attempts at reintroducing frequent low-intensity fires to prevent oaks, evergreen shrubs, and other hardwoods from crowding out the understory flora associated with the *P. palustris* forests in the southeastern United States, where less than 2% of the original forest remains (Means 1996). Mechanisms to limit the global movement of pests and pathogens are continuously being developed, such as those regulating the movement of wood packaging material. There remains a crucial need to improve quarantine and the transport of invasive alien microbes and insects that threaten pine ecosystems.

Rethinking and reorientation of management practices are needed to improve the health and resilience of pine-dominated ecosystems while also addressing human needs and values (e.g., Etienne 2000). Clearly formulated and pragmatic criteria are needed on where and when range expansions and/or densification is desirable or acceptable, and where and when management intervention is warranted. Reintroducing fire is crucial in many contexts, perhaps in conjunction with the removal of hardwoods, management of invasive species, and the reintroduction of rare or framework species of plants, animals, or microorganisms. Sensitive pine species could benefit from effective air pollution control programs aimed at reducing levels of criteria pollutants (ozone, sulfur, and nitrogen oxides or particulate matter) affecting human health. Beyond such purely ecological challenges, however, there is a pressing need for the development of more harmonious integration of forest and wildlife conservation, active, integrated management of ecosystems and landscapes, and ecological restoration where needed, especially in contexts where local people are motivated to participate. The key is to wed ecological and socio-economic values driving the various efforts (Aronson et al. 2007, Clewell & Aronson 2006).

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

D.M.R. and S.P. acknowledge financial support from the DST-NRF Center of Excellence for Invasion Biology. S.T.J.'s contribution was supported by the National Science Foundation (Ecology and Earth System History Programs). M.J.W. acknowledges the DST-NRF Center of Excellence in Tree Health Biotechnology. For help with preparation of figures, we thank Tom Swetnam (Laboratory of Tree-Ring Research, University of Arizona; **Figure 1**), Susan Schilling (USDA Forest Service Pacific Southwest Research Station; **Figure 2**), and Mary Anne McGuire (University of Georgia, School of Forestry and Natural Resources; **Figures 1** and **3**).

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Annual Review of
Ecology, Evolution,
and Systematics

Volume 38, 2007

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